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Maiden journey of fledgling emperor penguins from the Mawson Coast, East Antarctica

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ABSTRACT: The at-sea distribution of fledgling emperor penguins *Aptenodytes forsteri* is largely unknown. Seven and 10 fledglings, respectively, were satellite tracked on their maiden voyage from the colonies at Taylor Glacier in 1996 and from Auster in 2007. In both years, the young birds dispersed widely, well beyond the pack ice zone once they had left and reached open water. They spent a substantial part of their time north of 60° S, i.e. outside the Antarctic Treaty area. The northernmost latitudes reached were 54° 14′ S in 1996 and 56° 15′ S in 2007. Their longitudinal distribution ranged from 7 to 93° E. The fledglings did not congregate in particular feeding areas nor did they appear to be associated with oceanographic fronts or the sea ice in their first 2 to 3 mo at sea. Towards the beginning of winter, they changed course and headed south back towards the ice but not to their natal colonies.

KEY WORDS: Emperor penguins · Fledglings · Maiden voyage · Sea ice

INTRODUCTION

Emperor penguins *Aptenodytes forsteri* live and breed in one of Earth's most dynamic environments characterised by significant large-scale seasonal and inter-annual changes. The extent of the frozen ocean surfaces ranges from approximately 4 million km^2 in summer to approximately 20 million km^2 in winter (Allison 1989). This pulsation of retreating and extending ice makes the coastline of Antarctica a highly variable environment. The sea ice comprises 2 major zones: the fast ice and the pack ice. Extending north from the continent is the fast ice, a huge, continuous area of frozen ocean surface. All but 3 of the currently known breeding colonies of emperor penguins are located on the fast ice. The colonies are usually located at the southern part of the fast ice near the continent where it is comparatively stable, i.e. it persists until the end of the chick-rearing season. Should the fast ice break out prematurely, the survival of the chicks is at risk. Other than the duration of the fast ice, its extent is an important factor for the penguins as it determines the distance to foraging grounds (e.g. Barbraud & Weimerskirch 2001). Fast ice extent is highly variable between years, and reduced breeding success may be associated with above-average coverage of fast ice (see Massom et al. 2009).

While the fast ice offers a safe breeding surface, it also largely excludes the penguins from potential foraging areas. Occasionally, tide cracks appear in the fast ice that offer temporary and spatially limited access to the sea (e.g. Wienecke & Robertson 1997), or the penguins access polynyas, areas of open water in the fast ice, to forage (e.g. Ancel et al. 1992).

North of the edge of the fast ice lies the pack ice, a highly dynamic area where ice floes drift on the surface of the ocean. Its northern limit is highly variable on an inter-annual scale and is subject to the influence of storms and the presence and location of icebergs (e.g. Brunt et al. 2006).

The link between sea ice extent (total distance from the Antarctic continent to the northern edge of the pack ice) and events at the colony may be comparatively clear-cut. A question less clear is whether juvenile emperor penguins respond to changes in sea ice conditions, particularly when they first venture to sea. The fast ice may play a role because before accessing potential foraging areas, the young birds often have to

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traverse extended areas of fast ice. Thus, when leaving their natal colonies, fledgling emperor penguins face 2 formidable tasks: they must navigate long distances across the fast ice, and, once they reach the ice edge, they then have to decide where to go. Satellite technology allows us to observe their horizontal movements long after they have left the colony and, hence, determine their foraging ranges and examine the extent to which individuals may be influenced by sea ice conditions (e.g. Zimmer et al. 2008).

Tracking studies of juvenile penguins are still rare, possibly because of the comparatively high cost of the equipment and the certainty that the instruments cannot be retrieved. While adults must prepare for their annual moult in summer and return to moult locations in the coastal areas of Antarctica (e.g. Kooyman et al. 2000, Wienecke et al. 2004), young emperor penguins are not restricted by the demands of breeding. This offers an opportunity to examine how far they disperse and range from their colonies and expand our knowledge of the challenges young emperor penguins may face on their maiden voyage. Emperor penguin fledglings were first tracked from Cape Washington, Ross Sea, in 1994; from December 1994 until December 1997, 10 fledglings were followed by satellite, and a further 6 were tracked in 2001 (Kooyman & Ponganis 2008). To understand the factors that influence recruitment and ultimately the survival of a population, we need to focus our efforts on fledglings, determine their at-sea distribution and investigate the factors potentially influencing their distribution. The aims of this study were to (1) determine the extent of dispersal of fledgling emperor penguins on their maiden voyage, (2) establish whether they utilise common foraging areas, (3) examine how their at-sea movements may relate to current and sea ice conditions, and (4) ascertain how closely the young birds are associated with the pack ice. (5) We also wanted to learn whether they return to the continent in winter.

MATERIALS AND METHODS

Satellite tracking. On 17 December 1995, 7 satellite trackers were deployed on emperor penguin fledglings at the colony at Taylor Glacier (67° 28′ S, 60° 53′ E), and on 14 and 15 December 2006, we deployed 10 trackers on fledglings at the Auster colony (67° 23′ S, 64° 02′ E). We had planned to repeat the tracking at Taylor Glacier. However, deep snow, large tide cracks and highly rafted fast ice made it impossible to reach the colony in December 2006. All trackers were deployed on young penguins whose juvenal plumage was well developed. Prior to deployment, the fledglings were weighed. We chose the biggest chicks to carry the instruments, as in both years the juveniles had to traverse at least 40 km of fast ice from the colony to the ice edge. Thus, for several days the fledglings had to rely on their remaining body reserves for survival. The fattest chicks potentially have the highest chance to reach the ice edge.

The instruments used in 1995 were Telonics ST-10s, and in 2006 we used Sirtrack KiwiSats. To conserve battery power and extend the transmission period, all instruments were duty cycled; in 1995, the trackers transmitted every 90 s on a 24/48 h on/off schedule, and in 2006, the duty cycle was 4/44 h on/off transmitting once every 45 s. The instruments weighed 92 ± 2 g and were attached to the lower back with industrial strength contact glue (Loctite 401™) and 2 plastic cable ties.

Positions were obtained from Polar Orbiting Environmental Satellites operated by the National Oceanic and Atmospheric Administration (NOAA, USA) via the Argos Data Collection and Localisation System (Argos CLS, France). The Argos system separates locations into 6 categories (3, 2, 1, 0, A, B: best to worst) depending on the estimated accuracy of the location (see Service Argos 1996). Only positions of category A or better were included in these analyses, and any location that resulted in speeds of >10 km h^{-1} was eliminated. Location data were interpolated using the method of Wienecke & Robertson (1997) to give daily location estimates for each bird.

Sea ice data. Sea ice data were obtained from the National Snow and Ice Data Center (NSIDC), University of Colorado, Boulder, Colorado, USA. The analyses of regional sea ice data used by NSIDC are obtained from *in situ* meteorological and oceanographic observations, as well as from near real-time integration of remote sensing data. Standard analysis procedures were applied that take into consideration the variability in scale and resolution of the various data sets (Fetterer et al. 2002).

Penguin movements. Penguin movements were examined in relation to sea ice motion in 1996 and ocean surface currents in 2007. Due to the limited temporal coverage of the sea ice motion and ocean currents, we could not compare the penguin movement to sea ice motion for the 2007 tracking data nor to ocean currents for the 1996 tracking data. Daily sea ice motion data for the 1995/96 season were taken from satellite-derived estimates (Fowler 2003). Weekly data of ocean surface current for the 2006/2007 season were obtained from satellite-derived estimates produced by the Centre de Topographie des Océans et de l'Hydrosphère/Laboratoire d'Etudes en Géophysique et Océanographie (CTOH/LEGOS), France (Sudre & Morrow 2008).

The observed movements of the fledglings in relation to the pack ice movements were assessed using the following randomisation procedure. For every 6 h time step, the position of each bird was collated along with the expected position of that bird had it drifted passively with the sea ice from its previous position. The distance d_0 between the actual and expected-passive positions was calculated. The expected-passive position was then replaced with a new expected position at a random angle and distance from the previous day's position (using random distances varying from 0 to the actual distance of the expected-passive movement). The distance from this random position to the actual position was noted. This random-movement step was carried out 10 000 times in total, giving distances d_1 to $d_{10\,000}$. If the penguin's movement was related to the sea ice movement, one would expect that the distance d_0 would be smaller than most of the randomised distances d_1–$d_{10\,000}$. A conservative percentile threshold of 0.1 % was used, i.e. a penguin's movement during a given time step was deemed to be related to the sea ice motion if the distance d_0 was smaller than 99.9 % of the randomised distances d_1–$d_{10\,000}$. Penguin movements were compared to surface current movements using an identical procedure.

Statistics. Comparisons between years were made using 1-way analysis of variance (ANOVA) after passing tests for normality and equal variance. The Holm-Sidak method was applied to all multiple pairwise comparisons. When normality tests failed, Mann-Whitney rank sum tests were applied. The level of significance was set to <0.05 unless stated otherwise. All means are given ± 1 SD.

RESULTS

The tracking seasons were named after the year during which most of the tracking occurred. Thus, the 1995/96 season is referred to as 1996 and the 2006/07 season as 2007.

Fledgling body mass and deployment summary

At the time of deployment, the body mass of the emperor penguin fledglings averaged 15.6 ± 1.7 kg in December 1995 and 15.5 ± 1.7 kg in December 2006 (Table 1). Post-deployment, the fledglings remained in the colony for 1 to 5 d in 1995 and 2 to 10 d in 2006 before heading towards the ice edge. The fledglings were tracked for 28 to 160 d and 38 to 189 d in 1996 and 2007, respectively. The majority of juveniles (4 in 1996 and 6 in 2007) were tracked for >100 d (Table 1). They reached maximal distances of up to 1570 and 2343 km from their natal colonies in 1996 and 2007, respectively, and total distances travelled ranged from 862 to 7160 km (Table 1).

Distribution in relation to sea ice

Upon departure, the young penguins had to traverse 40 to 50 km of fast ice before reaching the pack ice in both tracking seasons. In 1996, the 7 fledglings took up

Table 1. *Aptenodytes forsteri*. Body mass, deployment and departure dates and distances of fledgling emperor penguins. Most northerly position of the fledglings, total time tracked after departing the colony and time and percentage spent north of 60° S are also shown

Fledgling	Body mass (kg)	Deployment date	Departure date	Date of last transmission	Total tracking distance (km)	Maximal distance from colony (km)	Northernmost latitude	Total time tracked (d)	Time at <60° S (d)	Percent of tracked time
1995/96										
1	16.8	17 Dec 95	22 Dec 95	16 Feb 96	2848	1299	58° 13.8' S	57	36	63
2	16.2	17 Dec 95	22 Dec 95	28 May 96	4919	1570	58° 35.4' S	159	57	36
3	18.0	17 Dec 95	22 Dec 95	22 May 96	5506	1472	54° 14.4' S	153	60	39
4	14.0	17 Dec 95	20 Dec 95	14 Jan 96	862	592	62° 39.6' S	28	0	0
5	13.0	17 Dec 95	19 Dec 95	25 May 96	7160	1041	58° 54.0' S	160	33	21
6	15.8	17 Dec 95	21 Dec 95	31 Jan 96	1554	1180	57° 24.0' S	41	18	46
7	15.5	17 Dec 95	18 Dec 95	3 Apr 96	4258	1149	57° 15.6' S	108	51	47
2006/07										
1	13.2	14 Dec 06	19 Dec 06	25 Feb 07	2250	1069	58° 03.0' S	70	20	21
2	16.2	14 Dec 06	17 Dec 06	30 May 07	6400	1557	56° 15.0' S	166	76	46
3	17.4	14 Dec 06	17 Dec 06	15 Mar 07	3035	966	57° 39.6' S	88	4	5
4	14.8	14 Dec 06	24 Dec 06	21 Jun 07	6780	2335	57° 10.2' S	178	68	38
5	13.8	14 Dec 06	22 Dec 06	24 Apr 07	4190	1455	60° 12.6' S	124	0	0
6	15.4	15 Dec 06	22 Dec 06	12 May 07	6565	1722	57° 57.0' S	142	54	38
7	13.5	15 Dec 06	22 Dec 06	28 Jun 07	5530	2343	62° 26.4' S	189	0	0
8	17.8	15 Dec 06	20 Dec 06	11 Feb 07	2025	859	59° 52.2' S	52	2	4
9	17.4	15 Dec 06	22 Dec 06	28 Jan 07	1375	926	59° 49.8' S	38	2	6
10	15.9	15 Dec 06	17 Dec 06	30 May 07	5845	1310	58° 13.2' S	165	34	21

to 3 to 4 d to reach the edge of the fast ice (Table 2). In comparison, in 2007, 4 fledglings (Nos. 2, 4, 6 and 7) tracked across the ice in 3 d but the others needed up to 8 d (Table 2). The longest crossing was performed in 2007 by Fledgling 8 as it added 2 d to its travels by initially marching towards the continent. About 20 km south-east of the colony, it turned and moved to the margin of the fast ice. Another fledgling went to the edge of the fast ice, then turned east and travelled along approximately 67° S until it reach 70° E, from where it headed north.

Once they reached the edge of the fast ice, the fledglings travelled northwards, moved through the pack ice and then dispersed widely in ice-free (<15% ice cover) water (Fig. 1). In both years, all fledglings had reached open water or an area with little pack ice by early to mid-January. The continental shelf off the Mawson Coast is rather narrow; the water reaches a depth of 1000 m some 100 km north of the 2 study colonies (Fig. 2). Thus, after leaving the waters above the continental shelf, the fledglings entered deep waters soon after they entered the pack ice.

Throughout February, all but 1 fledgling remained in oceanic waters >3000 m deep (Fig. 1), and many reached their maximal distance from the pack ice edge (see below).

In March 1996, the sea ice reached its minimal extent, while in 2007 it was already expanding again. In 1996, all fledglings were still either well north of or near 60° S while in 2007, 2 of the 7 birds with still operating transmitters were well south of this latitude. One of these had reached the northern edge of the pack ice at about 65° 24' S early in the month but returned to more northerly latitudes after about 2 d (Fig. 1).

In April of both years, the sea ice made significant northward advances, especially in the Prydz Bay region. The fledglings in this area had penetrated the pack ice zone or were approaching it. To the west, 2 of the fledglings tracked in 1996 were still at comparatively low latitudes. In 2007, 4 fledglings were west of 40° E; 2 had already reached the pack ice while the other 2 were heading straight for it (Fig. 1).

In May 1996 and 2007, the young penguins (n = 3 in 1996, n = 5 in 2007) returned to the ice, which was still expanding northwards. By June, Fledglings 4 and 7 reaching the most easterly latitudes in 2007 were in very heavy pack ice (90 to 100%), where they remained until the transmissions ceased at that time when both had turned north (Fig. 1).

The maximal distances from the pack ice varied among fledglings that were tracked for >100 d (n = 4 in 1996, n = 6 in 2007). In 1996, the 4 fledglings moved northwards as the sea ice retracted southwards (Fig. 3). This northwards movement was highly directed and was followed by an intermediate period where the distance between the birds and the pack ice remained generally >600 km. The fledglings reached their northernmost destinations in February and March. For example, in March 1996, Fledgling 3 was about 1200 km north of the pack ice edge. From late March to late April, the young penguins appeared to approach the pack ice quite rapidly (Fig. 3).

Table 2. *Aptenodytes forsteri*. Monthly total distances (km) travelled by emperor penguin fledglings. Number of days per month for which data were available is given in brackets

Fledgling	Dec: Fast ice	Dec: Pack ice	Jan	Feb	Mar	Apr	May	Jun
1995/96								
1	76 (4)	213 (6)	1323 (31)	696 (15)				
2	83 (4)	257 (7)	1068 (31)	994 (29)	906 (31)	804 (30)	892 (27)	
3	101 (4)	251 (6)	1379 (31)	1146 (29)	1152 (31)	979 (30)	527 (21)	
4	105 (4)	331 (11)	310 (13)					
5	114 (4)	352 (9)	1115 (31)	1013 (29)	1450 (31)	1023 (30)	1059 (24)	
6	81 (3)	331 (8)	1103 (30)					
7	78 (3)	257 (9)	1266 (31)	844 (29)	1563 (31)	47 (2)		
2006/07								
1	57 (5)	232 (7)	1173 (31)	684 (24)				
2	105 (3)	385 (11)	1547 (31)	1076 (28)	1104 (31)	1332 (30)	727 (29)	
3	122 (7)	273 (9)	1122 (31)	901 (28)	504 (14)			
4	40 (3)	131 (5)	1352 (31)	1085 (28)	1476 (31)	1367 (30)	798 (31)	455 (20)
5	70 (4)	161 (7)	829 (31)	719 (28)	1305 (31)	1021 (23)		
6	70 (3)	377 (7)	1764 (31)	1209 (28)	1344 (31)	1312 (30)	373 (11)	
7	49 (3)	258 (7)	888 (31)	1095 (28)	952 (31)	942 (30)	809 (31)	427 (27)
8	210 (8)	105 (3)	1245 (31)	398 (10)				
9	116 (6)	238 (5)	1057 (27)					
10	99 (4)	450 (11)	1012 (31)	1471 (28)	1123 (31)	966 (30)	516 (29)	

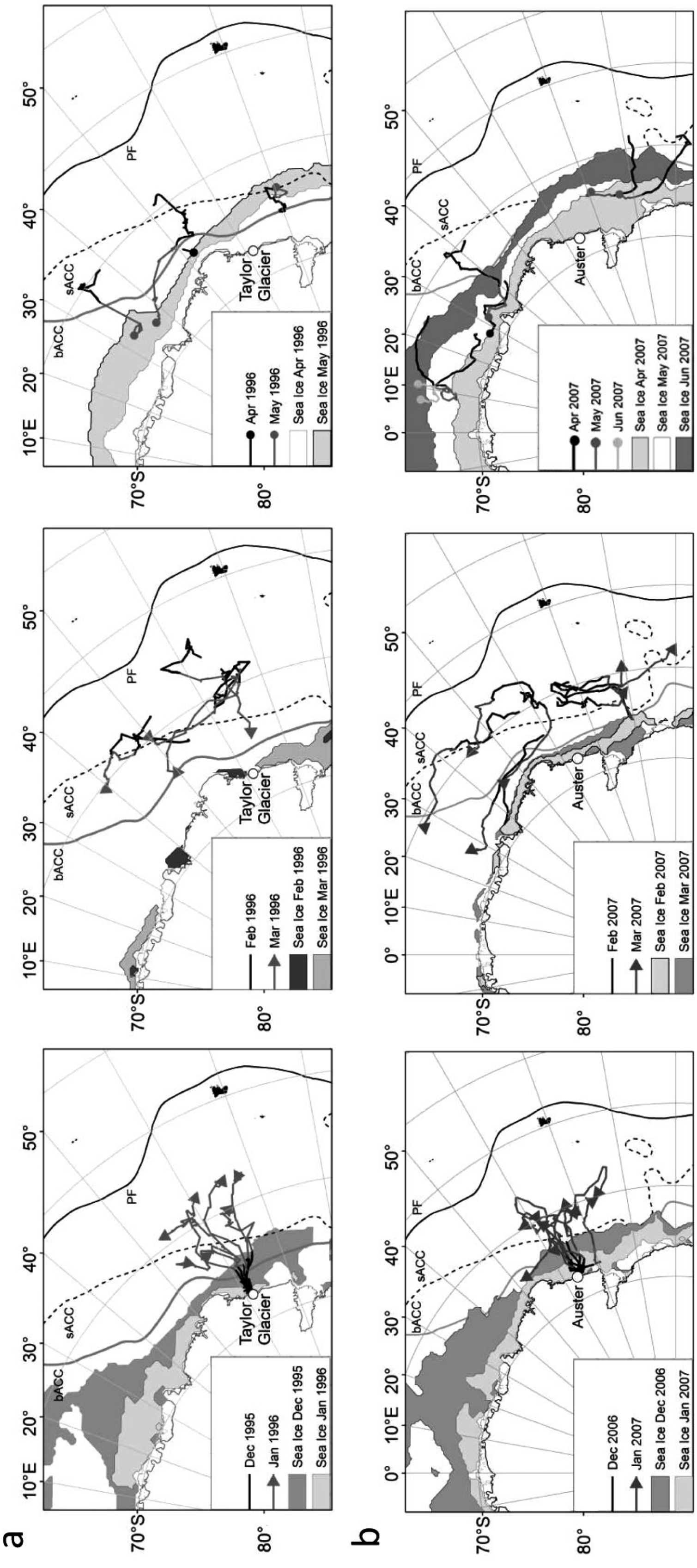

Fig. 1. *Aptenodytes forsteri.* Travels of emperor penguin fledglings tracked from (a) Taylor Glacier in 1996 and (b) Auster in 2007. Also shown is the maximal extent of the sea ice per month. The 3 major currents shown are the Polar Front (PF), the southern Antarctic Circumpolar Current front (sACC) and the southern boundary of the ACC (bACC)

In 2007, 2 fledglings (4 and 6) exhibited similar patterns to those observed in 1996 in that they rapidly increased their distance from the pack ice once they reached the open ocean. Fledgling 10 initially did the same but returned to the pack ice for about 2 d in late February before moving north again and reaching a distance of 600 km from the ice edge. The maximal distance from the pack ice reached by Fledgling 5 was just <600 km. In late February, it turned south and meandered relatively near (~100 km) the edge of the shelf ice near the continent. The remaining 2 birds behaved quite differently compared to the others in that they remained largely in an area approximately 100 to 200 km north of the pack ice zone, and also closer to the shelf break.

At-sea distribution. During the first 2 mo of the tracking period, the fledglings increased the distances from their natal colonies (Fig. 4). Particularly in 2007, there was a strong movement away from the point of origin and after just over 6 mo, 2 fledglings were >2300 km from their starting point.

In 1996, the fledglings from Taylor Glacier remained largely between 40 and 70° E during the tracking period. Some remained in the Cooperation Sea north of the Mawson Coast while others dispersed more widely (Fig. 1, Appendix 1). The most westerly location was reached by Fledgling 2 at 32° 37.8′ E, nearly 1600 km from its natal colony on 24 May. This bird had travelled westward in open water until 24 April, when it turned sharply south and moved towards the sea ice. Fledgling 3 reached the northernmost location in this study on 13 February 1996 when it was at 54° 14.4′ S some 53 d after leaving the colony. There was little dispersion to the east; only 1 fledgling passed 70° E (Fig. 1). The birds travelling westwards were above the Enderby Abyssal Plain where the water is 5000 m deep, or traversed the Haakon VII Sea (Fig. 2).

In 2007, the 10 fledglings from Auster dispersed more widely than the birds from Taylor Glacier in 1996. The most northerly position was reached by Fledgling 2 at 56° 15′ S. In their longitudinal dispersion, the fledglings from Auster ranged from 7 to 93° E, collectively covering virtually a quarter of the Southern Ocean in their first 6 mo at sea (Fig. 1). Four of the fledglings travelling westwards also ventured into the region of the Enderby Abyssal Plain or the Haakon VII Sea. Four others moved eastwards towards the south-

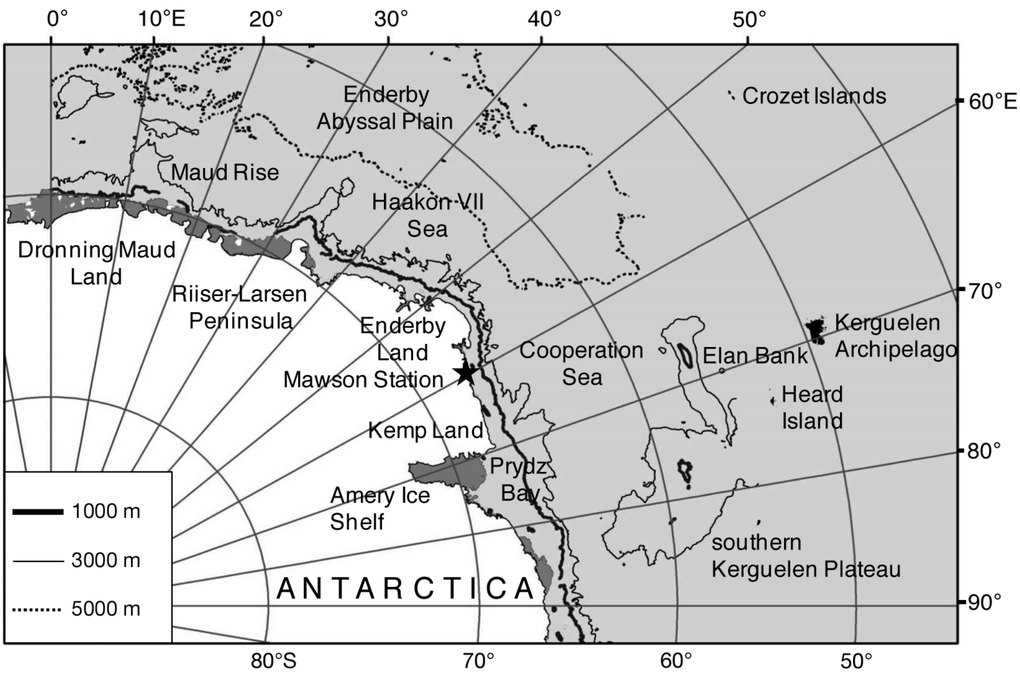

Fig. 2. Bathymetry off the coast of East Antarctica

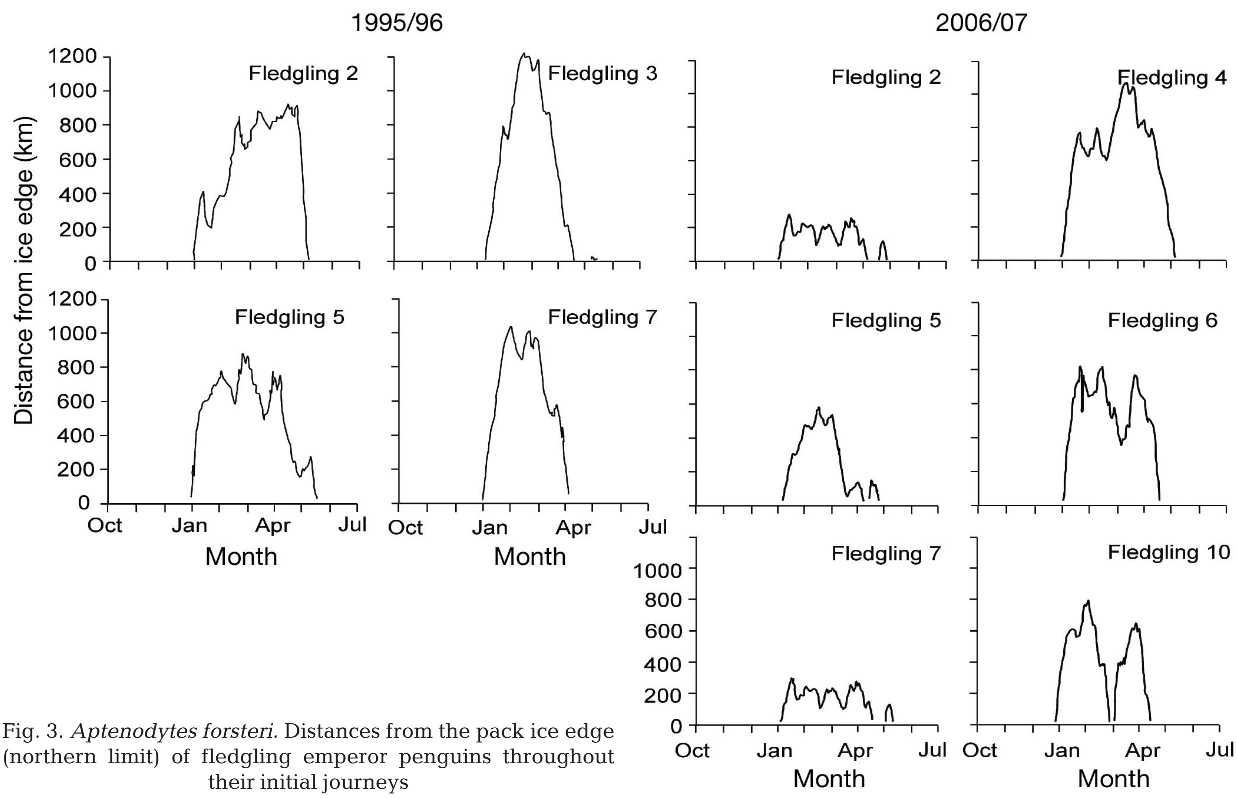

Fig. 3. *Aptenodytes forsteri.* Distances from the pack ice edge (northern limit) of fledgling emperor penguins throughout their initial journeys

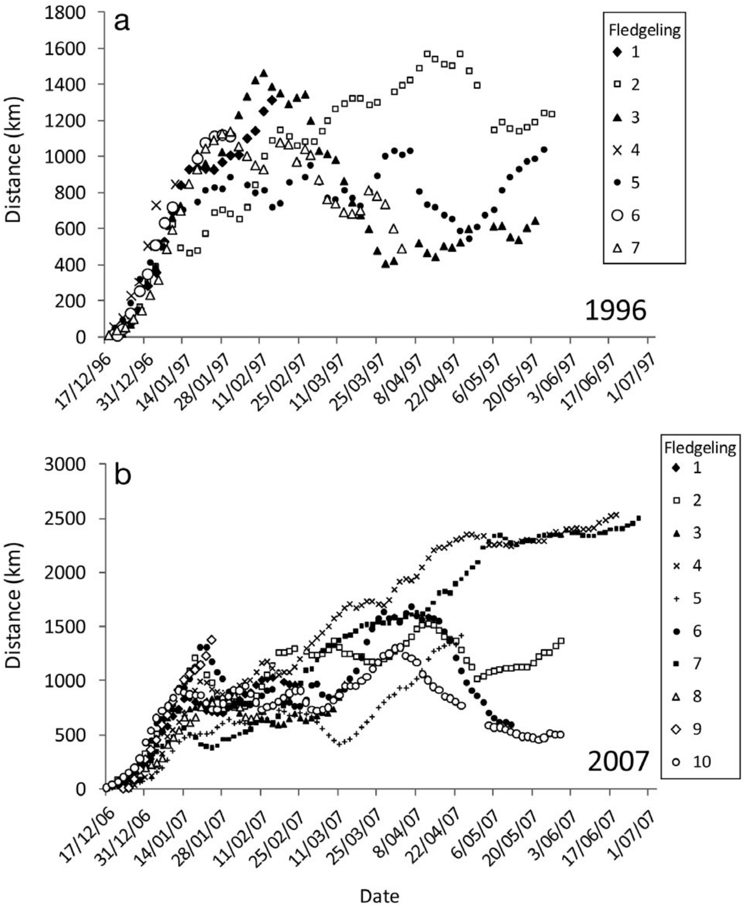

Fig. 4. *Aptenodytes forsteri.* Distances from the natal colonies of emperor penguin fledglings during their first few months at sea (a) 1996/97; (b) 2006/07

ern end of the Kerguelen Plateau east of Prydz Bay. While none of the fledglings in either year followed the shelf break (submerged offshore boundary of the continental shelf), 2 fledglings tracked in 2007 stayed much closer to the coast than the others (Fig. 1).

In both study years, most of the penguins spent extended periods north of 60° S, i.e. outside the region covered under Article VI of the Antarctic Treaty of 1959 (available at www.ats.aq/documents/ats/treaty_original. pdf): 11 of the 17 fledglings foraged outside the treaty area for 18 to 76 d, 3 spent <1 wk north of this latitude, while another 3 remained south of 60° S throughout the tracking period (Table 1, Fig. 1).

The timing of the return to the ice varied among the fledglings. Their initial northward movement terminated for most in mid- to late January and was overall more pronounced than their journey south (Fig. 5). The initiation of their return to the ice was variable, as was the time they took to reach the pack ice.

Travel speeds

In 1996, the fledglings progressed on average somewhat faster across the fast ice than in 2007 (Fig. 6). While the difference was not significant between years (t = 1.462, d = 15, p = 0.164), the speeds attained on the fast ice were significantly slower than in the pack ice in both years (1996:

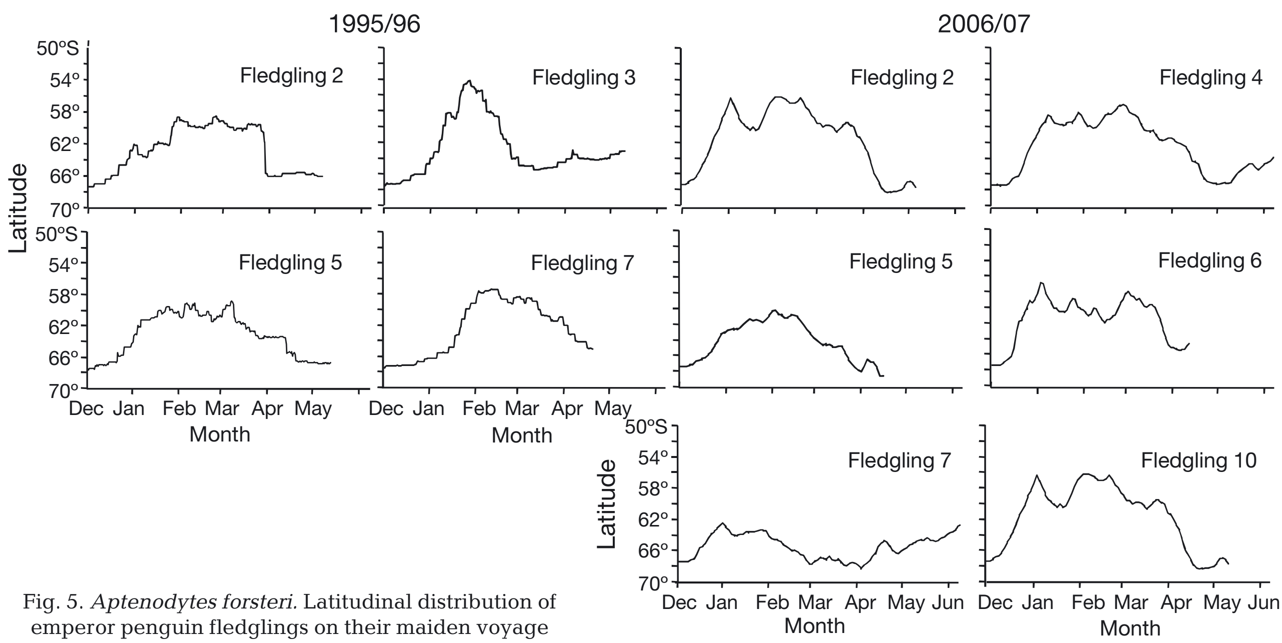

Fig. 5. *Aptenodytes forsteri.* Latitudinal distribution of emperor penguin fledglings on their maiden voyage

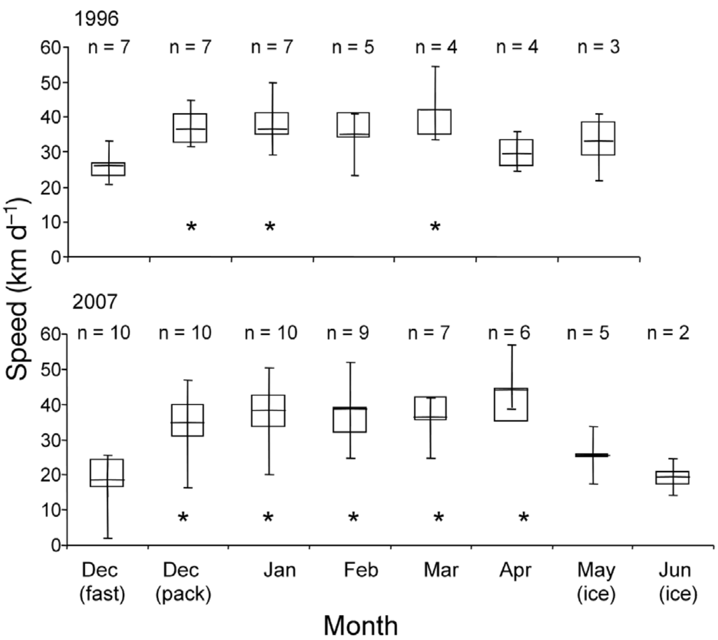

Fig. 6. *Aptenodytes forsteri.* Median daily travelling speeds (km d^{-1}) by month of emperor penguin fledglings during their first trip to sea. Lower and upper quartiles and interquartile ranges are also presented. Asterisks indicate significant differences ($p < 0.05$) of speeds within years

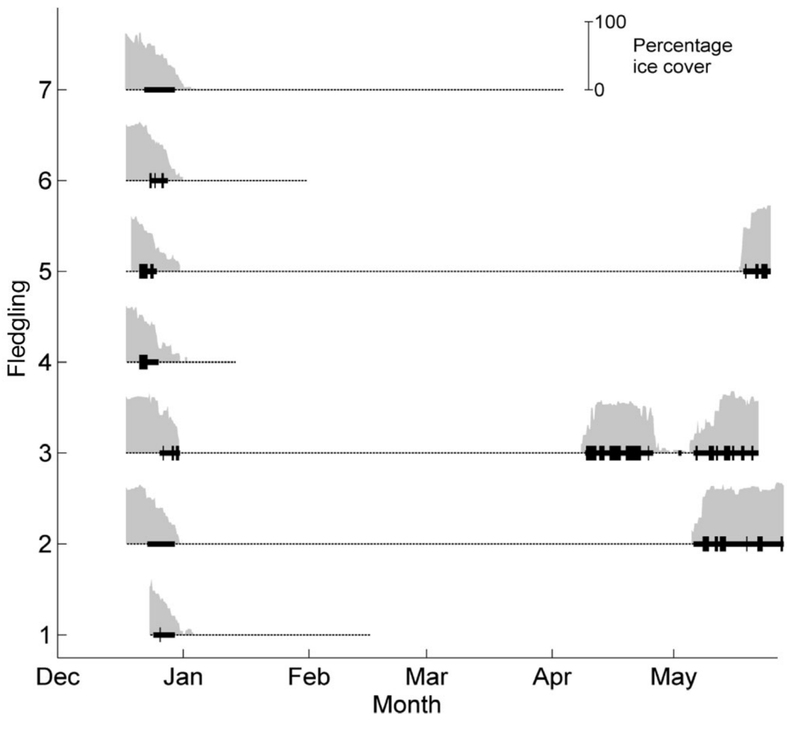

Fig. 7. *Aptenodytes forsteri.* Summary of penguin movements in relation to sea ice motion during 1996. Heavy black horizontal lines indicate days on which a penguin's movement was related to the sea ice motion; thinner black horizontal lines show when it was not. Thin dotted horizontal lines indicate periods during which the penguin was not in the sea ice zone, or for which sea ice motion data were not available at the penguin's location. Shaded area above each line indicates sea ice concentration (percentage cover)

$t = 4.002$, df = 2, $p = 0.017$; 2007: $t = 4.091$, df = 2, $p = 0.025$; see Appendix 2).

In 1996, the fledglings left the sea ice zone (fast ice plus pack ice zone) in 10 to 15 d, compared to 8 to 16 d in 2007. Once they reached open water, the average speeds ranged 37.0 ± 6.9 km d^{-1} in January to 40.9 ± 9.6 km d^{-1} in March (Fig. 6). The fledglings progressed significantly faster through the pack ice and in open water than when crossing the fast ice ($F = 4.136$, df = 6, 36, $p = 0.004$).

Similarly in 2007, the travel speeds remained consistent in the pack ice and in open water with 36.2 ± 9.3 km d^{-1} ranging from 37.5 ± 8.2 km d^{-1} in February to 40.3 ± 6.6 km d^{-1} in April. Again, these speeds were significantly faster compared to those achieved on the fast ice ($F = 8.076$, df = 7, 58, $p < 0.001$).

When the young penguins returned to the ice in April 1996 and in May 2007, they slowed down and were moving at speeds similar to those attained on the fast ice when they first left the colonies (1996: $U = 7.000$, $p = 0.230$; 2007: $t = -1.448$, df = 13, $p = 0.171$).

Movements in relation to pack ice motion and surface currents

In 1996, during their initial northward travel phase, the penguins' movements were generally not associated with the pack ice motion. However, 2 emperor penguin fledglings (2 and 3) travelled at times in the same direction as the moving pack ice early in the season when they departed the colony. Later in the season when the penguins returned to the pack ice, their movements were related to the pack ice motion for almost half of the time (124 of 254 six-hourly time steps; Fig. 7).

Fig. 8 illustrates 2 examples of a penguin's movement in relation to surface currents. From 14 to 20 January 2007, the movements of Fledgling 6 were closely related to the currents, particularly in the area where the current flow was quite strong. However, in the following week (21 to 28 January), the same penguin did not follow the current flow, appearing to avoid the strongest surface flow and at times moving in the opposite direction to the prevailing surface current. Overall, this mixed pattern of motion was consistently performed by all fledglings in 2007 (Fig. 9).

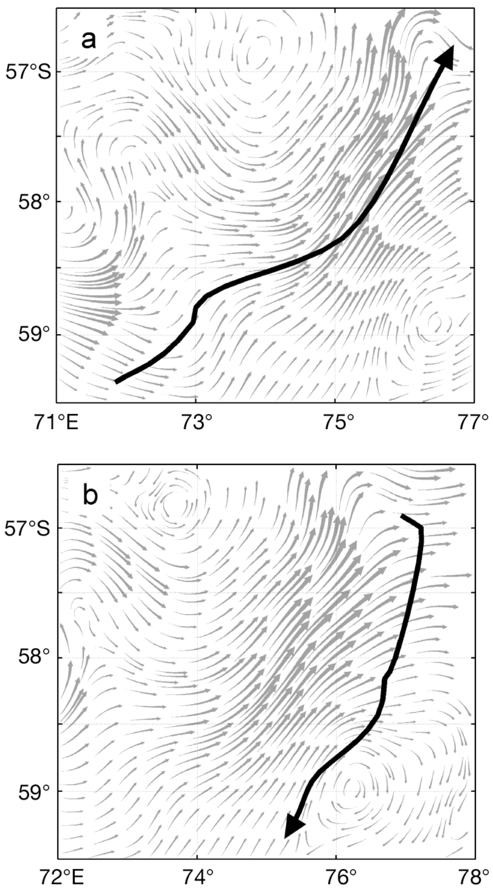

Fig. 8. *Aptenodytes forsteri.* Examples of penguin movements in relation to satellite-derived surface currents. (a) Fledgling 6, 14 to 20 January 2007, during which time the penguin's movements (black arrow) were related to surface currents (grey arrows; see 'Results'); (b) the same penguin during the following week (21 to 28 January), during which time its movements were not related to surface currents

DISCUSSION

Loss of instruments

Over the 2 study seasons, we deployed 17 satellite trackers. Three of those lasted <50 d, 4 transmitted from 50 to 100 d, and the remaining 10 were active for >100 d. Early termination of transmissions occurred most likely because the fledglings perished. Our attachment method has proven to be solid in past deployments on adult penguins when all instruments were retrieved of the penguins that returned to the colonies (see Wienecke & Robertson 1997, 2006, Wienecke et al. 2004). Thus, we consider the loss of instruments (i.e. detachment from the animal) unlikely. In terms of potential technical failures, these too are unlikely as the battery voltages were excellent, battery drain was within the expected range and the signal strengths were such that high class 1 and 2 fixes were delivered in the hours before the instruments ceased to operate.

Life expectancy in first-year emperor penguins may be as low as 20% (Williams 1995). We have no knowledge of the challenges young emperor penguins face on their maiden voyage. The deployment of satellite tags on fledglings tends to carry a higher risk than among adults because of the inexperience of the young birds and the lower life expectancy in their first year.

Distribution in relation to sea ice

The distances attained by young emperor penguins from the northernmost sea ice edge depend upon both the movements of the penguins and of the ice: as the penguins moved north in December, the pack ice continued to recede south. Similarly, in late autumn to early winter, when the penguins travelled south, the pack ice expanded north. These opposing movements explain at least in part the very strong trends shown in Fig. 3. On the other hand, it is apparent that most fledglings actively swam away from the pack ice edge and remained at significant distances for several months. Even those closest to the pack ice edge were still at least 100 km north of it.

After 2 to 3 mo in the open ocean, the fledglings returned to the ice. Due to their wide dispersion they reached the northern ice edge in different areas and at different times. The timing of the onset of their southern sojourn was highly asynchronous (see Fig. 5). Most fledglings returned gradually rather than suddenly to more southern waters. This raises the question of what cues the penguins may have reacted to when turning south and makes it likely that more than just changing light conditions provide the incentive. It was unexpected to find fledglings as deep in heavy pack ice as the 2 who were tracked until June 2007 (Fig. 1). They had already spent the month of May in the pack ice where the ice concentration was high. Whether they chose to stay there or were caught out by the rapidly advancing ice is unknown.

Distribution in relation to sea ice motion and surface currents

The data on sea ice motion have relatively large uncertainties. Heil et al. (2001) reported that satellite-derived estimates of motion (such as have been used here) can underestimate the true motion by up to 40%. In addition, errors that cannot always be quantified are

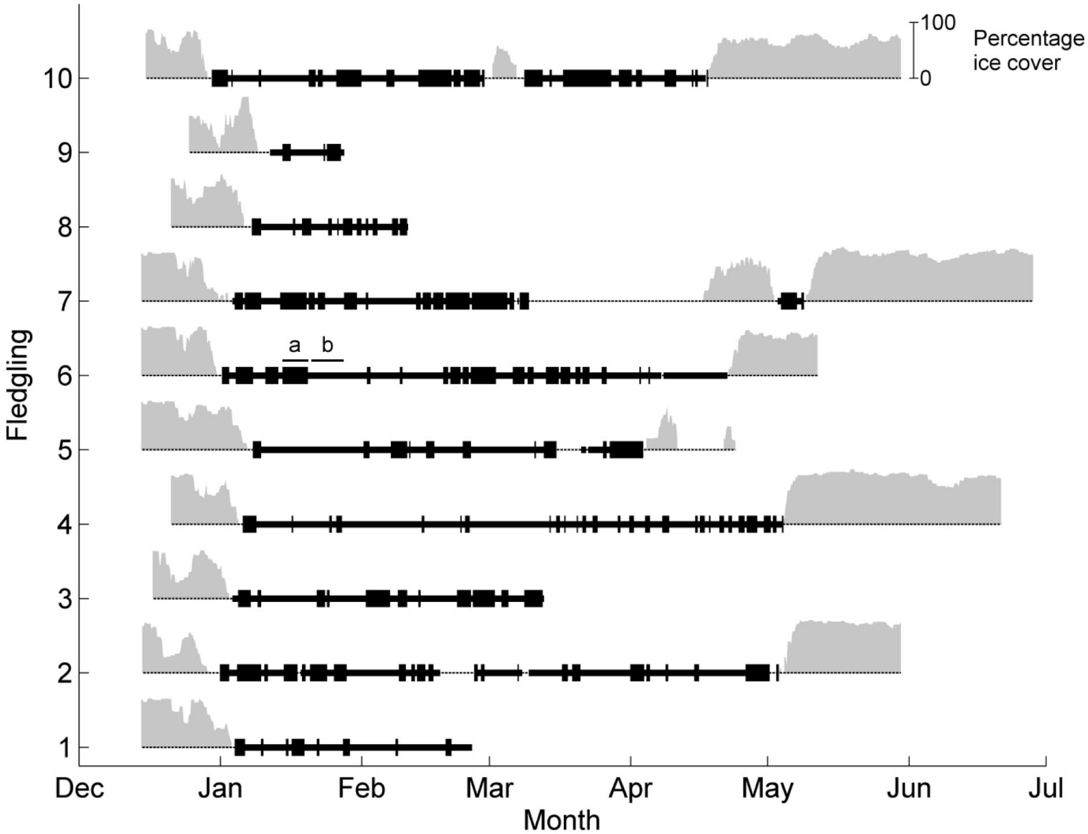

Fig. 9. *Aptenodytes forsteri*. Movements of emperor penguin fledglings tracked during 2007 in relation to surface currents. Symbology as in Fig. 7. Lines marked (a) and (b) indicate the periods corresponding to panels (a) and (b) in Fig. 8

associated with the location data of the penguins. Thus, it is not always feasible to distinguish an entirely passive motion of a hauled out penguin resting on a floe from the active movement of penguin still endeavouring to make independent progress across the surface of the ice. Active movement of the bird can only be discerned when the penguin moves noticeably faster than the pack ice. Where our results indicate that a penguin's movement was related to pack ice (or surface current) motion, it specifically means that the motion of the penguin was more closely related to the estimated pack ice motion than to simulated sea ice motion of a similar amplitude but in a random direction.

Speed and distances travelled in the fast ice zone were, as expected, slower than in the pack ice or the open water. On the fast ice, all movement is solely due to the activity of the penguins. However, in the pack ice and in the open water, there is some passive movement through wind and ocean circulation. In the pack ice zone, the fledglings can haul out onto to the ice and rest while the movement of the pack continues to transport them; buoys deployed in the Prydz Bay area travelled on average 14 km d^{-1} even in 90 to 100% density of pack ice (Allison 1989). The resolution of our tracking data is too coarse to investigate fine-scale movements. However, the distinct directional changes in the tracks of the penguins and daily average speeds exceeding the average current velocities of 20 to 30 km d^{-1} in southern parts of the fledglings' foraging area (Heil & Allison 1999) clearly indicate that they are not just drifting passively. For example, in 1996, Fledglings 4 and 5 initially left the colony and headed north towards the open water, but they travelled within areas where the pack ice also moved predominantly northwards. Thus, the birds' movements were similar to that of the pack ice. However, since the pack ice drifted at approximately 15 to 20 km d^{-1} (Heil & Allison 1999) and the 2 fledglings travelled 36 to 38 km d^{-1}, the motion of the penguins both in terms of direction of travel and speed was clearly determined by the birds, although the pack ice may have aided their movements.

The pack ice offers the penguins opportunities to haul out and rest, socialise and preen. Thus, they are likely to spend extended periods out of the water. That this happens is apparent from the better quality of positional data obtained while the birds were on the ice. Depending on the density of the pack ice, it can afford access to the ocean but also prevent penguins from hunting when wind and swell compress the floes. Under those circumstances, the penguins are forced to stay out of the water and might indeed drift with the ice, and the speed of travel should be no faster than that of the ice.

At-sea distribution

In both study years, the dispersal of emperor penguin fledglings was similar in that upon leaving the colonies, the young birds moved northwards before turning east or west. First, they crossed 40 to 50 km of fast ice in up to 8 d. Once they reached the pack ice they potentially had access to water. However, they still had to pass through at times very dense pack ice (about 200 km wide) before reaching open water.

The large-scale dispersal mainly occurred once the fledglings had reached or were near 60° S. Studies of the general patterns of the circulation of surface waters in East Antarctica indicate that between 60° and 90° E, a clockwise circulating gyre connects the waters of the continental shelf with the distant waters of the Antarctic Circumpolar Current (ACC; Smith et al. 1984). The northwards movement of this gyre broadly occurs off the Mawson Coast (Nicol 2006). Near 60° S, the gyre joins the ACC and starts turning south near 90° E as it is being deflected by the Kerguelen Plateau (e.g. Smith & Tréguer 1994, Nicol et al. 2006). This circulation may in part explain the initially strong northerly component of most of the fledglings' movements, as well as the eastwards travels in 2007.

Fledgling emperor penguins tracked from Cape Washington in the Ross Sea displayed some similarities in behaviours in comparison to those from the Mawson Coast. They, too, moved north to north-east, some reaching latitudes north of 60° S (Kooyman & Ponganis 2008). However, the movements of the fledglings from Cape Washington were far more consistent than those of their East Antarctic counterparts in that the northern passage was followed by a strong east to north-east movement. Another difference between the birds tracked from the Ross Sea and in East Antarctica was that the birds from the Ross Sea approached or even crossed the Antarctic Polar Front (APF), which defines the boundaries of the Southern Ocean in this region and in the southern Pacific Ocean. The APF is a region of maximal surface flow in the ACC (Hofmann 1985); the fledglings from the Ross Sea may have used this to their advantage and saved energy by moving along with the current and benefited from potentially rich foraging areas.

In contrast, throughout our study, all fledglings remained well south of the APF. In the southern Indian Ocean, the APF passes south of the Kerguelen Plateau (Park et al. 2008), >150 km farther north than the penguins' most northerly locations. However, the 2 oceanic fronts encountered by the penguins were the southern ACC front (sACC) and the southern boundary of the ACC (bACC; see Fig. 1; Orsi et al. 1995). The sACC, sometimes referred to as Antarctic Divergence (Deacon 1937), is an area of maximal wind stress between the westerly and easterly winds (Bindoff et al. 2000). The bACC represents the area of transition from the eastward movement of the ACC to the westwards flowing Antarctic Coastal Current (not shown in Fig. 1; Nicol et al. 2006). The fledglings foraging east of 60° E stayed largely in the eastward flowing waters between the APF and the sACC. Fledglings travelling westwards north of 66° S initially moved against the ACC, while others, also travelling west but staying south of the bACC, may have taken advantage of the coastal current.

During their extended periods north of 60° S, the fledglings are likely to consume different prey than in the higher latitudes. In East Antarctica, a major prey item for adult emperor penguins is the Antarctic silverfish *Pleuragramma antarcticum*, at least during the chick-rearing period (e.g. Wienecke & Robertson 1997). The northern limit of the distribution of the silverfish occurs around 60° S (Dewitt et al. 1990). However, the limited diving ability of the young penguins renders this neritic fish probably out of their reach. Their diet is likely to change from notothenid species typically found in relatively shallow waters to Antarctic krill *Euphausia superba* in the pack ice zone. Once they reach oceanic waters well north of the pack ice limit, it is highly possible that they consume, for example, lantern fish (Mycophidae) and perhaps squid, which are also a favourite prey among king penguins *Aptenodytes patagonicus* that forage in similar latitudes (Wienecke & Robertson 2006).

It took the fledglings the best part of 1 mo to reach their most northerly positions. Fourteen of the 17 fledglings passed 60° S, the latitude that defines the area relevant to the Antarctic Treaty of 1959. Eleven of the young penguins spent individually 21 to 63 % of the time they were tracked north of 60° S. Overall, 516 of a total of 1871 tracking days (about 28 %) were spent at latitudes <60° S where a similar behaviour was observed among fledgling emperor penguins departing from Cape Washington (74° 39′ S, 165° 25′ E) in the Ross Sea.

Kooyman et al. (1996) reported that 5 of the 6 birds tracked travelled as far as 56° 54′ S. One fledgling then appeared to follow the eastward flowing ACC north of 60° S until transmissions ceased. Kooyman et al. (1996) suggested that 60° S as a boundary for the area of responsibility for both the Antarctic Treaty and the Commission for the Conservation of Antarctic Marine

Living Resources (CCAMLR) may be too restricted for the protection of emperor penguins. This appears to apply to the regions of the Ross Sea and most of West Antarctica, where 60° S delimits both the Antarctic Treaty area, as well as the area of influence of CCAMLR. In contrast, in the southern Indian Ocean the mandate of CCAMLR extends to 45° S and, hence, encompasses the area where the fledglings from the Mawson Coast were foraging. As a regional fisheries management organisation with and ecosystem approach, CCAMLR needs to consider the needs of fledgling emperor penguins, especially early in their lives when they may be particularly vulnerable because their diving skills are not yet fully developed (Ponganis et al. 1999).

Our results highlight the importance of the oceanic areas of the Southern Ocean to emperor penguins. They may be less exclusively associated with the ice-zone than previously thought. This is true for fledglings, but also for post-breeding adults that ventured to about 62° S and spent considerable time in the open water while fattening up for the moult (Wienecke et al. 2004). Fledgling emperor penguins travel extraordinary distances in an environment essential alien to them, at least at the start of their journey. The total distances reported here are underestimates because of the coarse resolution of our data. At this stage it is impossible to determine the factors that influence the young penguins in their choice to go where they do. Clearly, there are several 'strategies' that work, as fledglings migrating to vastly different areas managed to survive for many months. The extraordinarily wide distribution of fledgling emperor penguins raises the question of how best to protect their food resources as the approach of establishing marine protected areas may not suit these penguins.

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LITERATURE CITED

Allison I (1989) The East Antarctic sea ice zone: ice characteristics and drift. GeoJournal 18:103–115

Ancel A, Kooyman GL, Ponganis PJ, Gendner JP and others (1992) Foraging behaviour of emperor penguins as a resource detector in winter and summer. Nature 360: 336–339

Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. Nature 411:183–185

Bindoff NL, Rosenberg MA, Warner MJ (2000) On the circulation of the waters over the Antarctic continental slope and rise between 80 and 150° E. Deep-Sea Res II 47: 2299–2326

Brunt KM, Sergienko O, MacAyeal DR (2006) Observations of unusual fast ice conditions in the southwest Ross Sea, Antarctica: preliminary analysis of iceberg and storminess effects. Ann Glaciol 44:183–187

Deacon GER (1937) The hydrology of the Southern Ocean. Discov Rep 15:3–152

Dewitt HH, Heemstra PC, Gon O (1990) Nototheniidae. In: Gon O, Heemstra PC (eds) Fishes of the Southern Ocean. J.L.B. Smith Institute of Ichthyology, Grahamstown, p 279–331

Fetterer F, Knowles K, Meier W, Savoie M (2002, updated 2008) Sea Ice Index. National Snow and Ice Data Center, Boulder, CO. Available at http://nsidc.org/data/g02135.html

Fowler C (2003, updated 2007) Polar Pathfinder daily 25 km EASE-grid sea ice motion vectors, December 1995–July 1996. National Snow and Ice Data Center, Boulder, CO. Available at: http://nsidc.org/data/docs/daac/nsidc0116_icemotion.gd.html

Heil P, Allison I (1999) The pattern and variability of Antarctic sea ice drift in the Indian Ocean and western Pacific sectors. J Geophys Res 104:15789–15802

Heil P, Fowler CW, Maslanik JA, Emery WJ, Allison I (2001) A comparison of East Antarctic sea ice motion derived using drifting buoys and remote sensing. Ann Glaciol 33: 139–144

Hofmann EE (1985) The large scale horizontal structure of the Antarctic Circumpolar Current from FGGE drifters. J Geophys Res 90:7087–7097

Kooyman GL, Ponganis PJ (2008) The initial journey of juvenile emperor penguins. Aquat Conserv Mar Freshw Ecosyst 17:S37–S43

Kooyman GL, Kooyman TG, Horning M, Kooyman CA (1996) Penguin dispersal after fledging. Nature 383:397

Kooyman GL, Hunke EC, Ackley SF, van Dam RP, Robertson G (2000) Moult of the emperor penguin: travel, location, and habitat selection. Mar Ecol Prog Ser 204:269–277

Massom RA, Hill K, Barbraud C, Adams N, Ancel A, Emmerson L, Pool MJ (2009) Fast ice distribution in Adelie Land, East Antarctica: inter-annual variability and implications for emperor penguins *Aptenodytes forsteri*. Mar Ecol Prog Ser 374:243–257

Nicol S (2006) Krill, currents, and sea ice: *Euphausia superba* and its changing environment. Bioscience 56:111–120

Nicol S, Worby AP, Strutton PG, Trull TW (2006) Oceanographic influences on Antarctic ecosystems: observations and insights from East Antarctica (0° to 150° E). In: Robinson AR, Brink KH (eds) The sea, Vol 14. Harvard University Press, Cambridge, MA, p 1493–1534

Orsi AH, Whitworth T III, Mowlin WDJ (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. Deep-Sea Res 42:641–673

Park YH, Roquet F, Durand I, Fuda JL (2008) Large-scale circulation over and around the Northern Kerguelen Plateau. Deep-Sea Res II 55:566–581

Ponganis PJ, Starke LN, Horning M, Kooyman GL (1999) Development of diving capacity in emperor penguins. J Exp Biol 202:781–786

Service Argos (1996) User manual. Service Argos, Washington DC

Smith N, Tréguer P (1994) Physical and chemical oceanography in the vicinity of Prydz Bay, Antarctica. In: El-Sayed SZ (ed) Southern Ocean ecology: the BIOMASS perspective. Cambridge University Press, Cambridge, p 25–43

Smith NR, Dong Z, Kerry KR, Wright S (1984) Water masses and circulation in the region of Prydz Bay. Deep-Sea Res 31:1121–1147

Sudre J, Morrow R (2008) Global surface currents: a high-resolution product for investigating ocean dynamics. Ocean Dyn 58:101–118

Wienecke B, Robertson G (1997) Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. Mar Ecol Prog Ser 159:249–263

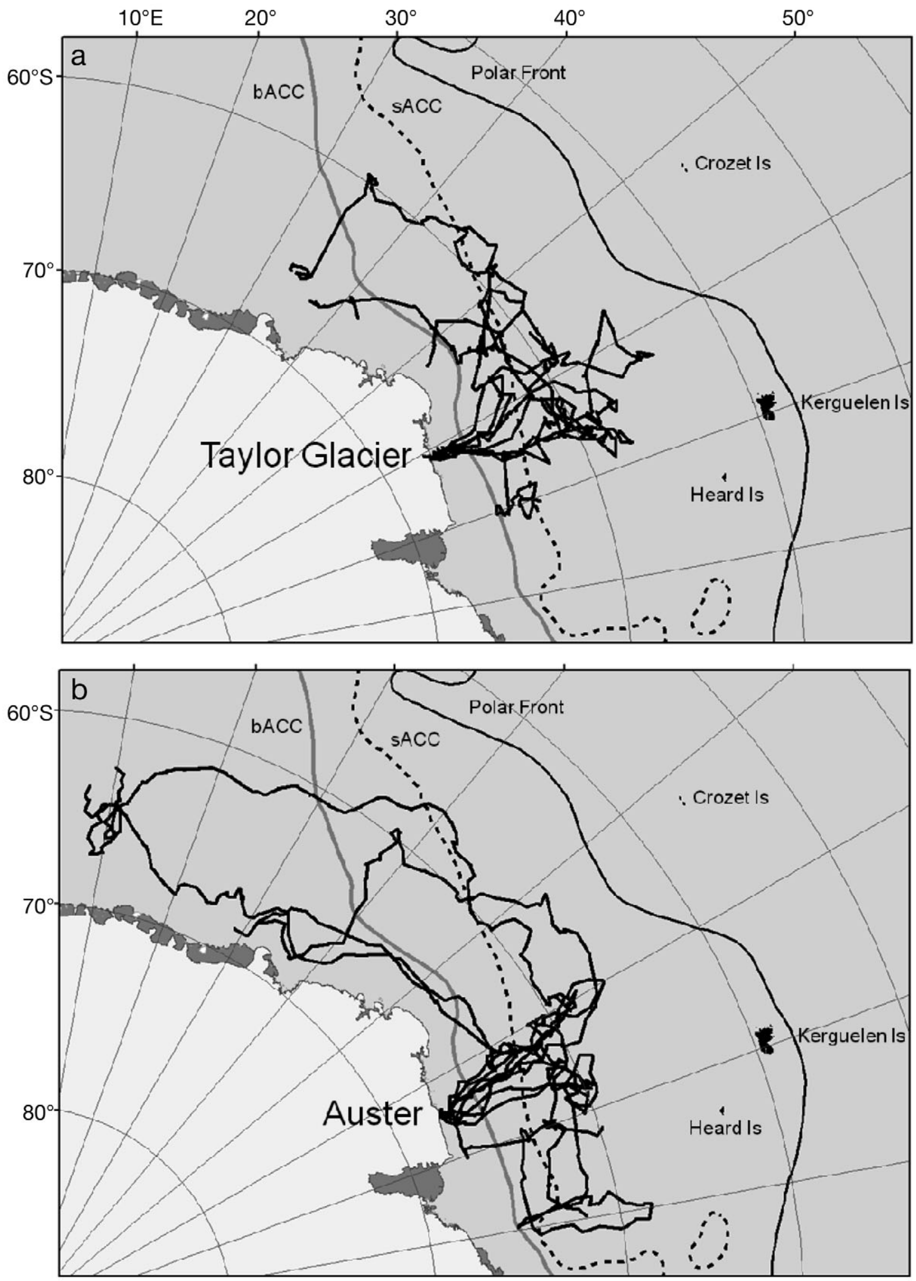
Wienecke B, Robertson G (2006) Comparison of foraging strategies of incubating king penguins *Aptenodytes patagonicus* from Macquarie and Heard islands. Polar Biol 29:424–438

Wienecke B, Kirkwood R, Robertson G (2004) Pre-moult foraging trips and moult locations of emperor penguins at the Mawson Coast. Polar Biol 27:83–91

Williams T (1995) Bird families: the penguins. Oxford University Press, Oxford

Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2008) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. Mar Biol 152:1187–1195

Appendix 1. *Aptenodytes forsteri*. Tracks of fledgling emperor penguins from (a) Taylor Glacier in 1995/96 and (b) Auster in 2006/07. Fronts shown are the Polar Front (black line), the southern Antarctic Circumpolar Current (sACC, dashed line) and the boundary current of the Antarctic Circumpolar Current (bACC, grey line)



Appendix 2. *Aptenodytes forsteri*. Mean (± SD) daily distances and speeds travelled by emperor penguin fledglings by month. The number of days per month for which data were available is given in brackets. Blank spaces = no data

Fledgling	Dec Fast ice km	Dec Fast ice km h^{-1}	Dec Pack ice km	Dec Pack ice km h^{-1}	Jan km	Jan km h^{-1}	Feb km	Feb km h^{-1}	Mar km	Mar km h^{-1}	Apr km	Apr km h^{-1}	May km	May km h^{-1}	Jun km	Jun km h^{-1}
1995/96																
1	18.9±8.9 (4)	0.8±0.4	35.5±12.5 (6)	1.5±0.5	42.7±18.7 (31)	1.8±0.8	20.7±6.1	46.4±10.0 (15)	1.9±0.4							
2	0.8±0.2 (4)	34.8±17.6	1.6±0.7 (7)	34.4±16.9	1.4±0.7 (31)	34.3±13.6	1.4±0.6 (29)	29.2±10.2 (31)	1.2±0.4	26.8±14.8 (30)	1.1±0.6	33.0±25.1 (27)	1.4±1.0			
3	25.3±24.4 (4)	1.1±1.0	41.9±10.1 (6)	1.7±0.4	44.5±16.7 (31)	1.9±0.7	39.5±16.5 (29)	1.6±0.7	40.4±17.1 (31)	1.7±0.7	32.6±13.0 (30)	1.4±0.5	25.1±11.9 (21)	1.0±0.5		
4	26.2±10.9 (4)	1.1±0.5	36.7±12.0 (9)	1.5±0.5	30.4±8.2 (13)											
5	28.5 ±19.5 (4)	1.1±0.4	42.0±7.7 (9)	1.6±0.7	36.0±35.3 (31)	1.5±0.8	34.9±35.3 (29)	1.5±0.7	46.8±46.6 (31)	1.9±0.5	34.1±34.8 (30)	1.4±0.8	44.1±44.0 (24)	1.8±0.8		
6	26.9±9.4 (3)	1.0±0.3	39.1±8.5 (8)	1.6±0.4	36.8±12.5 (30)	1.5±0.5										
7	19.4±20.5 (3)	0.8±0.9	28.5±13.7 (9)	1.2±0.6	41.9±14.3 (31)	1.7±0.6	30.2±17.0 (29)	1.3±0.7	51.4±13.3 (31)	2.1±0.6	45.9±1.3 (2)	1.9±0.1				
2006/07																
1	12.0±4.5 (5)	0.5±0.2	33.2±13.7 (7)	1.4±0.6	39.3±17.9 (31)	1.6±0.7	28.9±11.9 (24)	1.2±0.5								
2	26.2±9.2 (3)	1.1±0.4	35.0±12.1 (11)	1.5±0.5	51.6±14.4 (31) (28)	2.2±0.6	38.3±15.1 (31)	1.6±0.6	36.5±14.8 (30)	1.5±0.6	45.3±19.0 (29)	1.9±0.8	25.5±17.4	1.1±0.7		
3	17.4±5.3 (7)	0.7±0.2	30.4±6.4 (9)	1.3±0.3	36.5±20.8 (31)	1.5±0.9	33.1±18.6 (28)	1.3±0.8	37.7±13.1 (14)	1.6±0.5						
4	13.3±11.2 (3)	0.6±0.5	26.2±18.5 (5)	1.1±0.8	43.6±16.2 (31)	1.8±0.7	38.6±10.3 (28)	1.6±0.4	45.0±11.5 (31)	1.9±0.5	43.7±16.0 (30)	1.8±0.7	24.4±16.7 (31)	1.0±0.7	22.3±7.1 (20)	0.9±0.3
5	17.6±10.4 (4)	0.7±0.4	23.4±19.4 (7)	1.0±1.8	27.5±10.7 (31)	1.1±0.4	25.6±13.9 (28)	1.1±0.6	44.1±12.4 (31)	1.8±0.5	44.4±15.4 (23)	1.8±0.6				
6	20.0±5.6 (3)	0.8±0.2	53.9±31.2 (7)	2.2±1.3	58.5±23.2 (31)	2.4±1.0	44.9±18.8 (28)	1.9±0.8	43.8±16.7 (31)	1.8±0.7	43.9±20.2 (30)	1.8±0.8	33.9±11.4 (11)	1.4±0.5		
7	16.3±9.1 (3)	0.7±0.3	37.0±16.0 (7)	1.5±0.7	28.9±9.4 (31)	1.2±0.4	40.0±15.5 (28)	1.7±0.6	31.3±14.1 (31)	1.3±0.6	32.1±10.7 (30)	1.3±0.4	26.6±12.6 (31)	1.1±0.5	16.4±9.7 (27)	0.7±0.4
8	26.2±5.9 (8)	1.1±0.2	34.8±9.0 (3)	1.5±0.4	45.1±14.9 (31)	1.9±0.6	41.1±21.1 (10)	1.7±0.9								
9	17.5±12.7 (6)	0.7±0.5	47.4±2.6 (5)	2.0±0.1	37.3±13.8 (27)	1.6±0.6										
10	19.7±5.6 (4)	0.8±0.2	40.9±22.7 (11)	1.7±0.9	35.1±15.3 (31)	1.5±0.6	53.8±18.9 (28)	2.2±0.7	38.0±22.0 (31)	1.6±0.9	33.9±15.2 (30)	1.4±0.6	17.8±8.2 (29)	0.7±0.3		

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